Ecosystem engineering varies spatially: a test of the vegetation modification paradigm for prairie dogs

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Colonial, burrowing herbivores can be engineers of grassland and shrubland ecosystems worldwide. Spatial variation in landscapes suggests caution when extrapolating single-place studies of single species, but lack of data and the need to generalize often leads to 'model system' thinking and application of results beyond appropriate statistical inference. Generalizations about the engineering effects of prairie dogs (*Cynomys* sp.) developed largely from intensive study at a single complex of black-tailed prairie dogs *C. ludovicianus* in northern mixed prairie, but have been extrapolated to other ecoregions and prairie dog species in North America, and other colonial, burrowing herbivores. We tested the paradigm that prairie dogs decrease vegetation volume and the cover of grasses and tall shrubs, and increase bare ground and forb cover. We sampled vegetation on and off 279 colonies at 13 complexes of 3 prairie dog species widely distributed across 5 ecoregions in North America. The paradigm was generally supported at 7 black-tailed prairie dog complexes in northern mixed prairie, where vegetation volume, grass cover, and tall shrub cover were lower, and bare ground and forb cover were higher, on colonies than at paired off-colony sites. Outside the northern mixed prairie, all 3 prairie dog species consistently reduced vegetation volume, but their effects on cover of plant functional groups varied with prairie dog species and the grazing tolerance of dominant perennial grasses. White-tailed prairie dogs *C. leucurus* in sagebrush steppe did not reduce shrub cover, whereas black-tailed prairie dogs suppressed shrub cover at all complexes with tall shrubs in the surrounding habitat matrix. Black-tailed prairie dogs in shortgrass steppe and Gunnison's prairie dogs *C. gunnisoni* in Colorado Plateau grassland both had relatively minor effects on grass cover, which may reflect the dominance of grazing-tolerant shortgrasses at both complexes. Variation in modification of vegetation structure may be understood in terms of the responses of different dominant perennial grasses to intense defoliation and differences in foraging behavior among prairie dog species. Spatial variation in the engineering role of prairie dogs suggests spatial variation in their keystone role, and spatial variation in the roles of other ecosystem engineers. Thus, ecosystem engineering can have a spatial component not evident from single-place studies.

Ecosystem engineers affect physical and biological processes in grassland and shrubland habitats worldwide. Spatial variation in the inherent habitat matrix and functional variation among similar species of engineers may alter engineering processes, which can alter their keystone role. Colonial, burrowing herbivores can be both ecosystem engineers and keystone species that are widely distributed across diverse landscapes (Kotliar et al. 1999, Delibes-Mateos et al. 2011). Spatial variation in landscapes suggests caution before extrapolating single-place studies of single species, but lack of data and the need to generalize often leads to 'model system' thinking and application of results beyond appropriate statistical inference. Similarities in form and function of colonial, burrowing herbivores, and the ecosystems they engineer, suggest a model system approach is desirable, as it can generalize results from intensive studies of a single species at a single study site. Clearly, ecology benefits from this approach, but paradigms developed from intensive, single-place studies should be tested with extensive, multi-place studies.

Prairie dogs (*Cynomys* sp.) are colonial, burrowing, herbivorous rodents widely distributed in grasslands and shrublands of west-central North America. They have a complex social organization, with groups of families (coteries) comprising colonies, and groups of colonies comprising complexes (Hoogland 2006). Unsuitable or unoccupied land occurs within and among colonies; thus, complexes are a patchy aggregation of on- and off-colony sites. Prairie dogs are ecosystem engineers because they substantially modify the physical structure of vegetation and soils (Whicker and Detling 1988, Bangert and Slobodchikoff 2000, Davidson and Lightfoot 2008), and keystone species because they influence abundance, diversity, and population processes for many associated species (Kotliar et al. 1999,

Kotliar 2000), including birds (Baker et al. 2000, Smith and Lomolino 2004, Dinsmore et al. 2005), arthropods (Davidson and Lightfoot 2007), reptiles (Kretzer and Cully 2001), and other mammals (Stapp 2007, Cully et al. 2010). They also alter belowground structure, with effects that vary among species (Verdolin et al. 2008). Prairie dogs once occupied vast regions of central North America, but have been severely reduced in number and distribution by development, poisoning, plague (caused by *Yersinia pestis*), and recreational shooting. The black-tailed prairie dog (BTPD; *C. ludovicianus*), the Gunnison's prairie dog (GPD; *C. gunnisoni*), and the white-tailed prairie dog (WTPD; *C. leucurus*) are species of critical conservation concern that still occupy large complexes in several different ecoregions (Miller et al. 1994, Hoogland 2006, Slobodchikoff et al. 2009).

Our understanding of how prairie dogs modify vegetation structure developed largely from intensive studies of BTPDs in northern mixed prairie at Wind Cave National Park, South Dakota, USA. Studies there examined prairie dog effects on plant productivity, nutrient cycling, belowground structure, and shifts in vegetation composition and structure (Coppock et al. 1983, Archer et al. 1987, Polley and Detling 1988, Cid et al. 1991). The resulting paradigm was that prairie dogs create unique patches in the landscape with increased cover of bare ground and forbs, decreased cover of grasses, and decreased vegetation volume (Whicker and Detling 1988). Subsequent work demonstrated BTPDs reduced cover of tall shrubs in Texas (Weltzin et al. 1997) and Mexico (List 1997). This paradigm has been applied to other ecoregions, other species of prairie dog, and other species of colonial, burrowing herbivores (Stapp 1998, Delibes-Mateos et al. 2011). Spatial variation in the inherent habitat matrix among ecoregions, variation in foraging strategies among prairie dog species, and variation among other species and habitats suggests variation in engineering and keystone effects. For example, BTPDs live in dense social groups, build large burrow mounds, and clip vegetation both to remove and consume, whereas WTPDs live in sparse social groups, build small burrow mounds, and clip vegetation only to consume (Tileston and Lechleitner 1966). GPDs are intermediate, as they live in dense social groups but clip vegetation only to consume. Spatial variation in climate, soils, and other factors creates variation in the composition, height, canopy cover, and grazing tolerance of vegetation in the habitat matrix, which may mediate the effects of prairie dogs. For example, BTPD effects in arid shortgrass steppe can differ from those in more mesic northern mixed prairie (Stapp 2007, Hartley et al. 2009). Thus, the engineering role of prairie dogs relative to modification of vegetation structure may not apply equally across ecoregions and prairie dog species (Stapp 1998).

We tested the paradigm by asking how 3 species of prairie dogs in 5 ecoregions alter vegetation structure; specifically, do prairie dogs consistently increase cover of bare ground and forbs, and decrease vegetation volume and cover of grasses and tall shrubs. First, we examine variation within northern mixed prairie by assessing patterns at 7 BTPD complexes, with Wind Cave as the standard of comparison. Second, we examine variation among ecoregions and prairie dog species via 1 BTPD complex in shortgrass steppe of Colorado–Kansas, 1 BTPD complex in Chihuahuan Desert grassland of Mexico, 1 GPD complex in Colorado Plateau grassland of Arizona, and 3 WTPD complexes in sagebrush steppe of Colorado–Wyoming. We discuss spatial variation in prairie dog effects relative to dominant plants in the inherent habitat matrix, differences in foraging behavior among prairie dog species, and climatic gradients (e.g. aridity). Finally, we place our results within the ecological context of 1) prairie dogs as keystone species and 2) other ecosystem engineers, cognizant of the risk in generalizing beyond the scope of our results.

Methods

We sampled vegetation metrics both on and off 279 colonies at 13 prairie dog complexes in the United States and Mexico (Fig. 1) from May to July in 1996 (BTPD) and 1997 (GPD, WTPD). In both years, a field crew moved from south to north as each complex was sampled. Complexes were selected via expert opinion and located via agency maps; collectively, they represented most of the active, large BTPD, GPD, and WTPD complexes known to land managers and ecologists at the time of sampling. Complexes with many small (< 20 ha) or few (< 10) large colonies were not sampled due to logistical constraints and objectives related to concurrent studies (e.g. bird abundance). The Wind Cave complex (6 colonies) was included because it was the standard of comparison in this study.

The climate, soils, topography, and vegetation that comprised the inherent vegetation matrix surrounding these complexes varied regionally (Appendix 1). Complexes were analyzed by The Nature Conservancy ecoregions (TNC 1999), which were updated from Bailey (1995). For consistency with Great Plains literature (Coupland 1992, Lauenroth et al. 1999), we use northern mixed prairie for the northwestern Great Plains (Western Great Plains steppe of TNC) and shortgrass steppe for the west-central Great Plains (central shortgrass prairie of TNC). This terminology reflects greater aridity in shortgrass steppe relative to northern mixed prairie (Lauenroth et al. 1999).

We sampled 7 BTPD complexes (141 colonies) in northern mixed prairie (all dominated by perennial cool-season grasses, such as *Pascopyrum smithii*, and perennial warm-season shortgrasses, such as *Bouteloua gracilis*), 1 BTPD complex (13 colonies) in shortgrass steppe (dominated by perennial warm-season shortgrasses, such as *B. gracilis* and *Buchloe dactyloides*), 1 BTPD complex (28 colonies) in Chihuahuan Desert (dominated by perennial warm-season grasses, such as *Pleuraphis mutica*, and shrubs, such as *Prosopis glandulosa* and *Ephedra trifurca*), 1 GPD complex (15 colonies) in Colorado Plateau (dominated by *B. gracilis*), and 3 WTPD complexes (82 colonies) in sagebrush steppe (dominated by *Artemisia* and perennial and annual cool-season grasses; Fig. 1, Appendix 1). Of the 7 northern mixed prairie complexes, the 4 in South Dakota lacked a tall shrub component and were wetter (mean annual precipitation 43.1 cm), and the 3 in Wyoming and Montana had herbaceous cover similar to South Dakota, but were more arid (mean annual precipitation of 32.4 cm) and had a tall
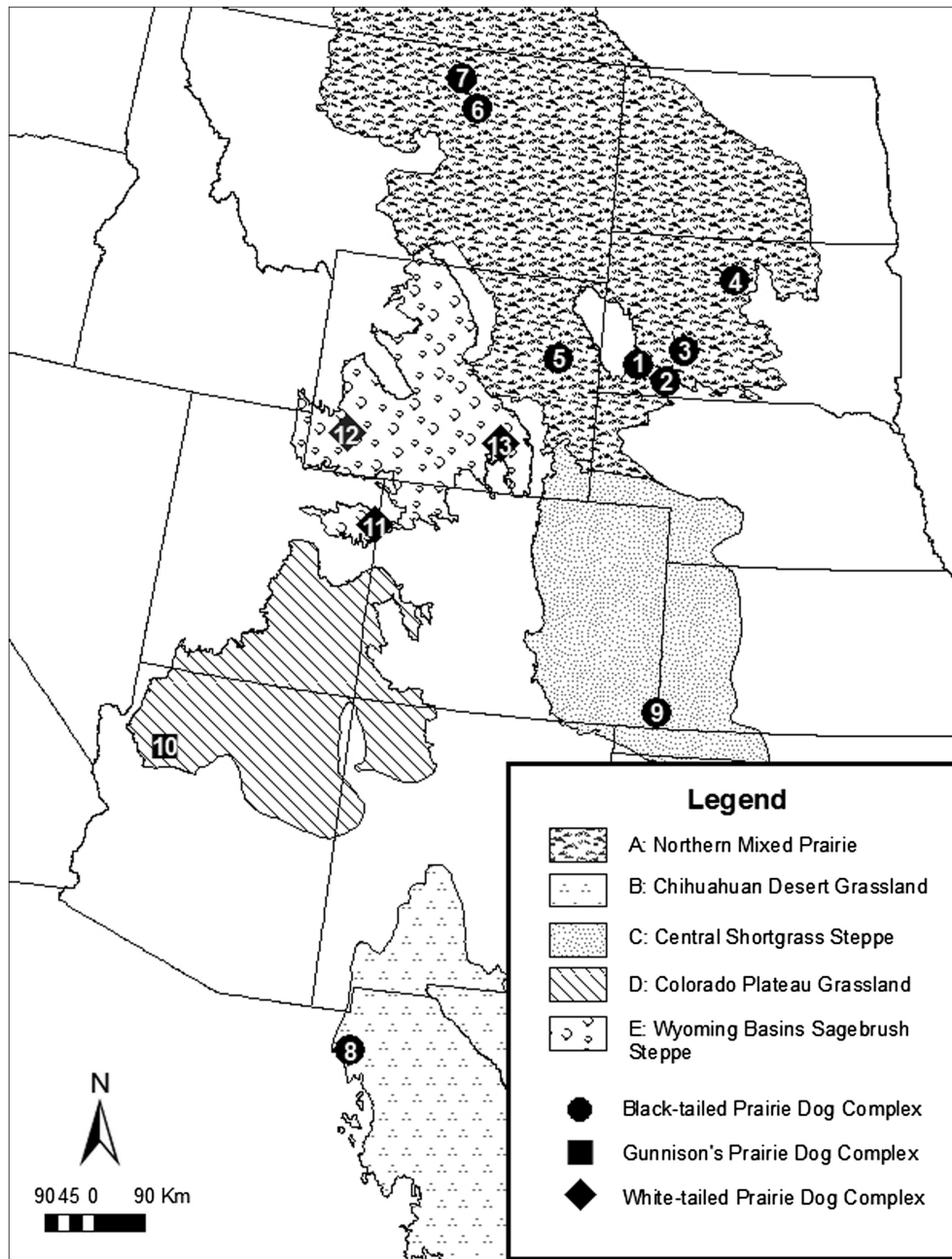
Figure 1. Locations of 13 complexes of 3 prairie dog species where vegetation attributes were measured in western North America. Complexes are shown relative to 5 ecoregions (A–E) whose boundaries were delineated through The Nature Conservancy's ecoregional planning process (TNC 1999). 1 = Wind Cave National Park; 2 = Pine Ridge Indian Reservation; 3 = Badlands National Park and Buffalo Gap National Grassland; 4 = Cheyenne River Indian Reservation; 5 = Thunder Basin National Grassland; 6 = Phillips County Public Lands (Bureau of Land Management [BLM] and C. M. Russell National Wildlife Refuge); 7 = Fort Belknap Indian Reservation; 8 = Janos – Casas Grandes region of Chihuahua, Mexico; 9 = Comanche and Cimarron National Grasslands; 10 = Aubrey Valley, Big Boquillas Ranch; 11 = Coyote Basin Public Lands (BLM and Dinosaur National Monument); 12 = Moxa Arch Public Lands (BLM); 13 = Shirley Basin Public Lands (BLM).

shrub component, primarily *Artemisia tridentata* and *A. cana*. All complexes were grazed by domestic cattle except Wind Cave and the Badlands portion of Badlands–Buffalo Gap, which were national parks grazed by bison *Bison bison*.

At each complex, colonies were selected using agency maps and were >20 ha in size and active at the time of sampling (prairie dogs or fresh scat present at burrows). Paired off-colony sites were located by observing colony boundaries, and identifying nearby (~0.5–2.0 km) sites with similar topography, soils, and current grazing management, but lacking prairie dogs. We sampled all colonies within a complex that met these criteria, with the exception that we sampled about half of the colonies at the 2 largest complexes due to time constraints (Badlands–Buffalo Gap and Thunder Basin). We assumed that on- and off-colony sites

had similar vegetation potential and that differences in vegetation were correlated with differences in prairie dog occupancy. Colony age and prairie dog density was unknown, but likely varied greatly. Recent rainfall and other weather patterns also influenced the state of vegetation present when we sampled. All complexes were sampled under conditions of average to above average moisture availability, with the exception of Janos–Casas Grandes, Mexico, which was sampled during a drought (Appendix 1; Palmer drought index for the month and year when sampled, National Climatic Data Center (<www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers.php>).

We sampled vegetation along a single transect that bisected each on and off colony site (mean transect length = 1300 m). Visual obstruction of vegetation (VO) and absolute canopy cover data were measured at a sampling station located every 100 m along transects. We visually estimated the absolute canopy cover of graminoids (grasses and *Carex* spp.), forbs, shrubs (including cacti), and bare ground within two 20×50 cm quadrats per sampling station (i.e. 28 quadrats on a 1300-m transect) (Daubenmire 1959). Quadrats were not moved if they occurred on burrows. We also recorded VO at 2 locations (adjacent to quadrats) per sampling station following the method of Robel et al. (1970), with the modification that increments on the pole were 2.5 cm. VO measurements at each location were obtained by observing the 1.5-m-tall pole from 1 m high and 4 m away in 4 perpendicular directions and recording the highest 2.5-cm interval completely obscured by vegetation (bare ground = 0) (i.e. 112 VO measures on a 1300-m transect). VO integrates both the horizontal and vertical planes as a surrogate of vegetation volume. For complexes of BTPDs, we visually estimated shrub canopy cover within a 0.1-ha plot (17.8-m radius) centered at each sampling station because we expected shrubs would be widely dispersed. For complexes of WTPDs and GPDs, we used the 20×50 cm quadrats (0.001-ha) to estimate shrub cover because we anticipated greater values at these sites. We estimated cover in categories (%) consisting of 0, 0–1, 1–5, 5–25, 25–50, 50–75, 75–95, and 95–100; midpoints were used for data analysis. We collected measurements from a total of 7553 sampling stations (15 106 quadrats and 60 428 VO measurements).

All statistical analyses treated the on-off colony pair as the unit of replication; therefore, we calculated a mean of vegetation metrics for each response variable on each transect. An analysis of variance (ANOVA; SAS Proc GLM ver. 6, SAS Inst.) was used to model variation among sites both with and without an effect of prairie dog presence included in the model. Residuals of all ANOVA's were examined for normality and homogeneity of variance, and if necessary, a power transformation was selected that maximized the Shapiro–Wilk statistic testing for normality of the residual errors (SAS Proc Univariate ver. 6; SAS Inst.). For each analysis, we fitted models with and without the effect of prairie dogs, calculated AICc values as an intermediate step, and then calculated and reported Akaike weights (w_i) comparing the 2 models (Burnham and Anderson 2002). Akaike weights represent the weight of evidence in favor of the model being the best model given that 1 of the models must be the best in that set.

Results

Variation in BTPD effects in northern mixed prairie

The paradigm that prairie dogs increase bare ground and forb cover and decrease VO, grass cover, and tall shrub cover was generally supported at 7 BTPD complexes in northern mixed prairie (Fig. 2). At Wind Cave (complex no. 1), bare ground was higher ($\overline{X} = 28$ vs 6%) and VO and grass cover were lower (1.6 vs 6.9 cm and 35 vs 76%, respectively) on colonies than at paired off-colony sites; these patterns were remarkably consistent in direction, magnitude, and strength of AIC evidence for all 7 complexes. Forb cover was higher on colonies at 6 of 7 complexes, including Wind Cave (16 vs 9%), but strength of evidence was weak at Wind Cave and 2 other complexes. Shrub cover was minimal and did not differ on and off colonies at the 4 South Dakota complexes, including Wind Cave (Fig. 2; no. 1–4). Shrub cover was lower on than off colonies at the 3 complexes in Montana and Wyoming (Fig. 2; no. 5–7), which had tall sagebrush (*A. tridentata* and *A. cana*) in the habitat matrix (Appendix 1).

Variation among prairie dog species and ecoregions

The paradigm was not generally supported for prairie dog species and ecoregions outside the northern mixed prairie (Fig. 1, 2). The only consistent prairie dog effect was lower VO on colonies at all 13 complexes. Thus, vegetation on prairie dog colonies was short and sparse relative to the inherent habitat matrix for all prairie dog species and ecoregions, but other effects varied.

For BTPDs in the Chihuahuan Desert (complex no. 8), bare ground dominated the landscape due to extreme drought conditions, but cover of bare ground was still higher on than off colonies ($\overline{X} = 90$ vs 80%). Grass cover was lower on than off colonies and was dominated by perennials. Although annual grasses and forbs were largely absent when we sampled, they can be abundant following summer rains. VO and shrub cover were much lower on than off colonies; honey mesquite *Prosopis glandulosa* was the dominant shrub. Thus, for BTPDs in Chihuahuan Desert the paradigm was largely supported, but the magnitudes of effect for bare ground and grass cover were less than in northern mixed prairie.

For BTPDs in the shortgrass steppe (complex no. 9), VO was slightly lower on than off colonies, but evidence was weak for an on-off difference in either bare ground or grass cover. Forb and shrub cover were nearly absent both on and off colonies. Thus, the only similarity between BTPD effects in shortgrass steppe and northern mixed prairie was that VO was reduced in both ecoregions.

For GPDs in the Colorado Plateau (complex no. 10), patterns were very similar to BTPDs in shortgrass steppe. VO was slightly lower on than off colonies within a matrix of short, sparse vegetation, but evidence was lacking for on-off differences in bare ground, grass cover, or forb cover. As in the shortgrass steppe (complex no. 9), grasses were dominated by blue grama *Bouteloua gracilis*, a grazing-tolerant shortgrass species (Appendix 1).
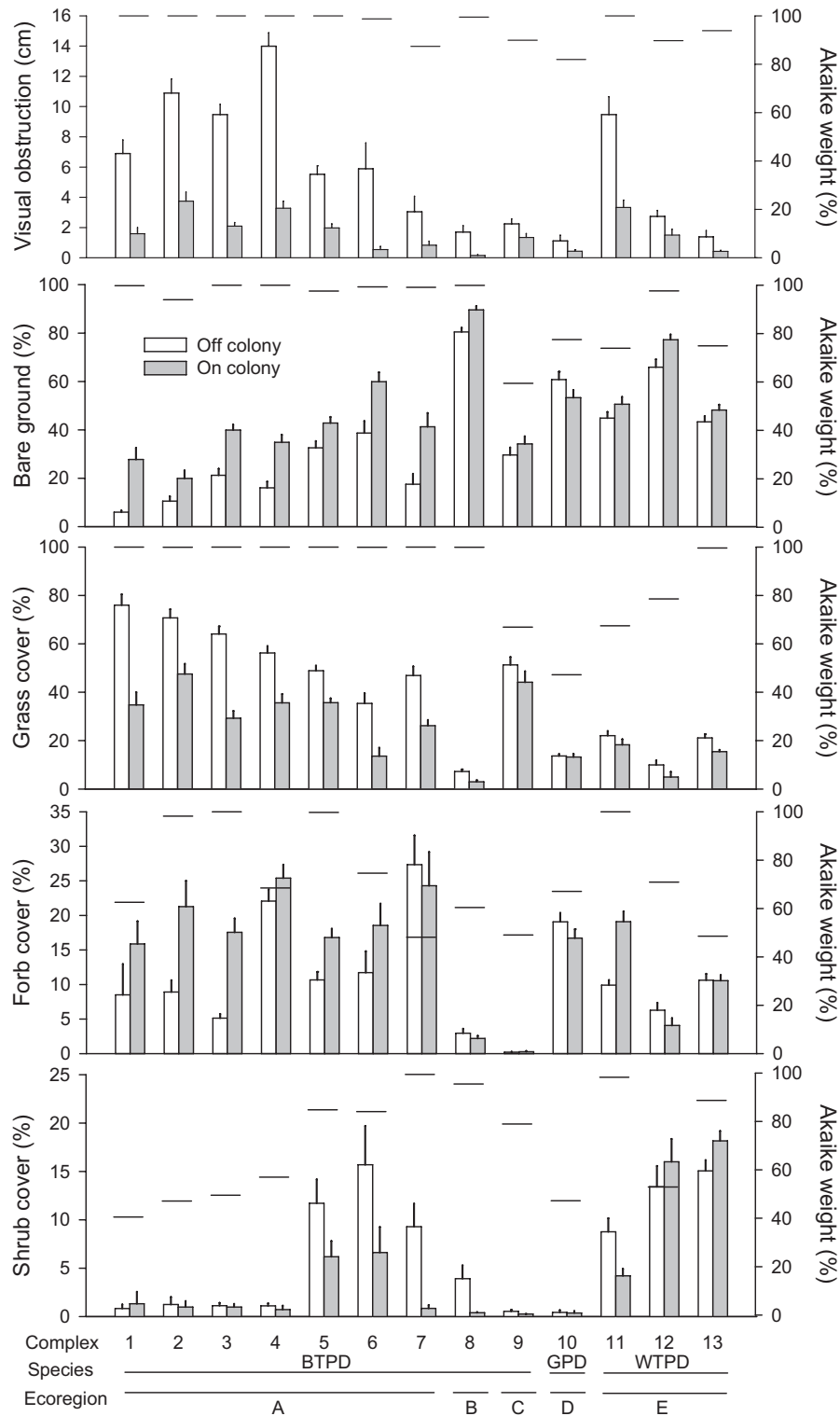
Figure 2. Comparison of 5 vegetation attributes measured off (open bars) and on (shaded bars) 279 prairie dog colonies at 13 complexes of 3 prairie dog species located in 5 ecoregions (Fig. 1). Akaike weight (0–100%) in support of a difference shown with horizontal bars; ± 1 standard error shown with vertical bars.

For WTPDs in the sagebrush steppe (complex no. 11–13), VO was lower on than off colonies at all 3 complexes. However, effects on bare ground, grass cover, and forb cover were weak and inconsistent. Shrub cover was lower on

than off colonies at complex no. 11, but was slightly higher on colonies at complex no. 12 and 13. Shrubs at all 3 complexes were dominated by tall species, such as *A. tridentata*. Weak effects of WTPDs on tall shrubs in sagebrush steppe

are in sharp contrast to strong BTPD effects on tall shrubs in both northern mixed prairie (complex no. 5–7) and Chihuahuan Desert (complex no. 8).

Discussion

Spatial variation in prairie dog engineering effects

The paradigm that prairie dogs increase cover of grasses and bare ground, and decrease cover of forbs and tall shrubs, was not consistently supported for all 3 prairie dog species and 5 ecoregions. However, visual obstruction (VO) was consistently lower on colonies at all 13 complexes; thus, prairie dogs created patches of short, sparse vegetation within a matrix of relatively tall, dense vegetation. Taken together, prairie dog colonies and off-colony sites increase heterogeneity and create diversity in the landscape. Generally, spatial variation in prairie dog engineering effects can be understood in terms of variation in dominant grass species, prairie dog species, and precipitation patterns.

In northern mixed prairie, BTPDs dramatically decreased grass cover and vegetation volume and increased bare ground. The consistency of prairie dog effects across the northern mixed prairie was striking given variation in the habitat matrix due to precipitation, soils, and plant species composition. Interestingly, *Pascopyrum smithii* was the dominant grass species at all 7 northern mixed prairie complexes. *Pascopyrum smithii* is a perennial, cool-season grass that exhibits phenotypic and genetic changes under prairie dog grazing, including increased leaf blade/sheath ratios and more horizontal leaf angles (Detling and Painter 1983, Polley and Detling 1988). Furthermore, productivity and below-ground reserves often decline under repeated grazing (Polley and Detling 1988, Milchunas et al. 2008). Thus, a finding of less vegetation volume, less grass cover, and more bare ground on colonies is consistent with the direct response of *P. smithii* to intense grazing, and with a lack of shifts in the height or cover of other plant species that might offset its response.

One of the most notable differences among prairie dog species was in their effect on shrub cover. BTPDs substantially reduced shrub cover both in the northern mixed prairie, where tall *Artemisia* shrubs dominated the 3 western complexes, and in the Chihuahuan Desert, where honey mesquite dominated the habitat matrix. In sharp contrast, WTPDs did not reduce shrub cover in sagebrush steppe, which had a similar composition of tall *Artemisia* shrubs as the 3 western BTPD complexes. We suggest the differential effect on tall shrubs between WTPDs and BTPDs is due to differences in life history traits. BTPDs live in more dense social groups and clip tall vegetation both to remove (presumably to facilitate predator detection) and consume, whereas WTPDs live in relatively sparse social groups and typically clip vegetation only to consume (Tileston and Lechleitner 1966). We regularly observed that BTPDs had removed and left uneaten 5–10 cm sections of *A. tridentata* stems, a species that declines under heavy browsing (Bilbrough and Richards 1993). We did not observe similar patterns for WTPDs. Dietary differences

among prairie dog species also may underlie their differential effects on shrub cover, but few comparative data exist. We also note that BTPDs in Chihuahuan Desert grassland significantly suppressed shrub cover, which consisted primarily of *P. glandulosa* and *E. trifurca*. Since our study, these shrubs have expanded where former prairie dog colonies have contracted (Ceballos et al. 2010); for example, there was a 14% increase in mesquite during the 8 yr following the poisoning of a prairie dog colony (List 1997). Similarly, in southern mixed prairie of Texas, BTPDs girdle and destroy mesquite seedlings and saplings, which restricted shrub invasion into former grassland (Weltzin et al. 1997).

White-tailed prairie dogs decreased vegetation volume nearly as much as BTPDs even though they did not decrease shrub cover and had relatively small effects on bare ground, grass cover, and forb cover. These patterns likely reflect the growth form of dominant herbaceous species in the sagebrush steppe habitat of WTPDs. Under the defoliation regime imposed by WTPDs, perennials such as *Elymus lanceolatus*, *Pleuraphis jamesii*, *Aristida* spp., and *Phlox hoodii*, as well as annual grasses and forbs, appear capable of maintaining a prostrate growth form with a similar amount of cover as off-colony vegetation. Thus, differences in prairie dog effects in sagebrush steppe versus northern mixed prairie reflect a combination of the differences in the foraging and clipping behavior of BTPDs and WTPDs, and differences in herbaceous plant responses to defoliation.

Prairie dog effects on grass and bare ground cover were reduced in the more arid sagebrush steppe, shortgrass steppe, Colorado Plateau, and Chihuahuan Desert relative to the northern mixed prairie. Reduced prairie dog effects in arid environments likely reflect seasonal differences in the timing and amount of precipitation and increased grazing tolerance of dominant herbaceous plants. Grazing and aridity often function as convergent selective forces, such that traits conferring plant resistance to aridity also confer greater grazing tolerance (Milchunas et al. 2008, Quiroga et al. 2010). Both the shortgrass steppe and Colorado Plateau are dominated by the grazing-tolerant shortgrass, *Bouteloua gracilis*, which is capable of sustaining basal and prostrate foliar cover under heavy grazing pressure. This contrasts with the taller *P. smithii*, which has a lower relative tolerance to repeated defoliation (Milchunas et al. 2008). Other studies in shortgrass steppe dominated by *B. gracilis* also reported reduced effects of BTPD on vegetation height and bare ground relative to northern mixed prairie (Winter et al. 2002, Stapp 2007, Hartley et al. 2009). Furthermore, both our study and Bartz et al. (2007) found only a modest difference in vegetation cover on and off GPD colonies in the Colorado Plateau (where *B. gracilis* is dominant), whereas Davidson and Lightfoot (2008) found larger effects of GPDs on grass cover and vegetation height in Chihuahuan Desert (where *B. gracilis* is not dominant). Mechanisms other than response of the dominant plant species may underlie these patterns, but research is lacking in part because GPDs are declining in number and persist only in relatively small and isolated complexes (Wagner et al. 2006). However, our study and others show how prairie dog effects can vary among species and ecoregions, which suggests the vegetation modification paradigm does not have universal application.

Finally, factors beyond the scope of this investigation likely mitigate prairie dog effects on vegetation. For example, plague can reduce the size and persistence of prairie dog colonies, which can reduce the magnitude of vegetation effects (Augustine et al. 2008, Hartley et al. 2009). At the time of our study, plague effects varied from recent (complex no. 9) to unaffected (South Dakota complexes) to unknown. In general, colonies can remain in the same location following recovery from plague (Wyoming and Montana) or move location (shortgrass steppe; Augustine et al. 2008). In shortgrass steppe, less vegetation in the habitat matrix, greater grazing resistance of dominant shortgrasses, and less frequent occupancy of prairie dogs in a given location due to plague epizootics may all contribute to reduced prairie dog effects on vegetation structure. In this study, we focused on spatial variation but ignored temporal variation. Inter-annual variation in precipitation influences vegetation structure in the habitat matrix, which likely influences prairie dog effects. Thus, plague, temporal variation, and other factors likely influenced prairie dog effects observed in this study of spatial variation.

Spatial variation in the keystone role of prairie dogs

How does spatial variation in the engineering role of prairie dogs apply to their keystone role? Vegetation volume was lower on than off colonies at all 13 complexes despite spatial variation in the habitat matrix. Colonies occurred as relatively homogenous patches of short, sparse vegetation within a more heterogeneous matrix; thus, prairie dogs increased heterogeneity at the landscape scale. Spatial heterogeneity in vegetation structure is a key factor contributing to diverse faunal communities, and has been closely linked to habitat for grassland and shrubland birds (Fuhlendorf et al. 2006, Derner et al. 2009).

Spatial variation in prairie dog effects likely affects associated fauna. For example, the mountain plover *Charadrius montanus* is a grassland bird species that breeds in areas with short, sparse vegetation. In sagebrush steppe, where bare ground cover already is high in the vegetation matrix, mountain plovers can be found in areas both with and without prairie dog disturbance (Plumb et al. 2005). In contrast, where the vegetation matrix is more dense, mountain plovers occur at higher densities (shortgrass steppe, Augustine 2011) or almost exclusively (northern mixed prairie; Dinsmore et al. 2005) on prairie dog colonies.

Shifts in vegetation structure induced by prairie dogs may also influence small mammal (Stapp 2007, Cully et al. 2010), large mammal (Krueger 1986), arthropod (Davidson and Lightfoot 2007), and herpetofaunal communities (Kretzer and Cully 2001). Specifically, Cully et al. (2010) found BTPDs consistently altered rodent species composition at many of the same complexes as in our study, with effects that varied along latitudinal and longitudinal gradients. In addition to effects on vegetation structure, prairie dogs affect associated species via development of burrow systems and serving as prey for a variety of species. Placed in context with previous prairie dog research, our large-scale study shows that spatial variation in how prairie dogs modify vegetation structure should be considered as one of several interacting effects that underlie spatial variation in the keystone role of prairie dogs.

Spatial variation in other ecosystem engineers

Given observed spatial variation in vegetation modification by prairie dogs, what patterns can be predicted for other ecosystem engineers? Colonial, burrowing herbivores occur on most continents, and like prairie dogs, are often considered ecosystem engineers. In Argentina, the plains vizcacha *Lagostomus maximus* is a colonial, burrowing rodent of semiarid scrub and grassland that decreases height and cover of grasses and shrubs, increases forb cover, and provides habitat for associated species (Branch et al. 1996). In Mongolian steppe, the colonial, burrowing Siberian marmot *Marmota sibirica* creates distinct patches within the grassland matrix, increasing complexity at the landscape scale (Van Staalduinen and Werger 2007). In Europe, the warrens and grazing activities of European rabbits *Oryctolagus cuniculus* increase plant heterogeneity and species richness (Gálvez-Bravo et al. 2011). In Australia, the burrowing bettong *Bettongia lesueur* is a colonial, burrowing marsupial that formerly was widespread and abundant in semi-arid and arid mainland. Before declining in abundance, they reduced shrub encroachment and likely altered vegetation structure in ways similar to prairie dogs (Baker and Noble 1999).

As with prairie dogs, we may expect to find spatial variation in vegetation modification by these species, which in turn is linked to their keystone effect on associated taxa. Our findings provide a baseline to evaluate variation among and within species relative to effects on vegetation structure in different ecosystems. Given similarities in engineering and keystone roles among colonial, burrowing herbivores across continents, and spatial variation in how prairie dogs modify vegetation structure, we suggest understanding spatial variation is critical to fully understanding the engineering and keystone effects of many other species.

Conclusions

We found that BTPD effects on vegetation structure in northern mixed prairie cannot be consistently extrapolated to other ecoregions or prairie dog species. Black-tailed prairie dog effects on grass cover and bare ground were less in shortgrass steppe and Colorado Plateau grassland than in northern mixed prairie. This may be explained by the dominance of grazing-tolerant shortgrasses in the matrix vegetation of shortgrass steppe and Colorado Plateau versus the dominance of taller-structured perennial grasses in northern mixed prairie. With respect to variation among prairie dog species, where shrubs occur in the matrix vegetation, shrub cover was consistently lower on BTPD colonies but not WTPD colonies. Differences may be due to greater burrow densities of BTPDs and their behavior of cutting shrubs to enhance visibility. In spite of spatial variation in their effects, all 3 species of prairie dog significantly reduced vegetation volume in all 5 ecoregions. We suggest that future efforts to understand prairie dog effects focus on sagebrush

steppe, shortgrass steppe, and desert grasslands, especially relative to the distribution of dominant plant species, the length of prairie dog occupancy, and temporal variation in precipitation patterns. Furthermore, spatial variation in how prairie dogs modify vegetation structure may be important in understanding how prairie dogs modify associated faunal communities. Vegetation modification should be integrated with other ways that prairie dogs influence associated species, including effects on belowground structure via burrowing, role as a prey source, and interactions with large herbivores.

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Appendix 1

Summary of dominant plant species, mean annual precipitation (MAP), Palmer drought index (PDI), number of colonies sampled, and mean values (repeated here from Fig. 2, see figure for error estimates and AIC results) for 5 vegetation attributes measured off and on 279 colonies at 13 prairie dog complexes in western North America. Complexes are organized by prairie dog species and ecoregion; see Fig. 1 for details.

| | Dominant plant species | | | MAP (cm)[d] | PDI[e] | No. colonies sampled | Cover (%) | | | | | | | | Visual obstruction (cm) | |
| | Grass[a] | Forbs[b] | Shrubs[c] | | | | Grass | | Forbs | | Shrubs | | Bare ground | | | |
							Off	On	Off	On	Off	On	Off	On	Off	On
Black-tailed prairie dogs, Northern Mixed Prairie																
1–Wind Cave, SD	PASM, BOGR, HECO	COCA, DYPA, SPCO	ARFR	45.2	>4	6	76	35	9	16	1	1	6	28	6.9	1.6
2–Pine Ridge, SD	PASM, BUDA, BRJA	SPCO, MEOF, DYPA	ARFR	40.3	>4	15	71	48	9	21	1	1	11	20	10.9	3.7
3–Badlands-Buffalo Gap, SD	PASM, BOGR, BRJA	COCA, HEHI, DYPA	ARFR	41.8	>4	27	64	29	5	18	1	1	21	40	9.5	2.1
4–Cheyenne River, SD	PASM, BUDA, BRTE	VIAM, PLPA, SPCO	ARFR	45.3	>4	33	56	36	22	25	1	1	16	35	14.0	3.3
5–Thunder Basin, WY	PASM, VUOC, BRTE	LOAR, SPCO, VIAM	ARTR	37.0	2 to 4	32	49	36	11	17	12	6	33	43	5.5	2.0
6–Phillips County, MT	PASM, BOGR, POSE	PLPA, VIAM, SPCO	ARTR, ARFR	31.8	−2 to 2	16	35	14	12	19	16	7	39	60	5.9	0.6
7–Fort Belknap, MT	PASM, BOGR, POSE	SEDE, PLPA, VIAM	ARCA, GUSA	28.5	2 to 3	12	47	26	27	24	9	1	18	41	3.0	0.8
Black-tailed prairie dogs, Chihuahuan Desert Grassland																
8–Janos-Casas Grandes, Mexico	PLMU, BOGR, BOCU	PLPA, DEPI	PRGL, EPTR	31.0	−3 to −4	28	7	3	3	2	4	0.4	80	90	1.7	0.1
Black-tailed prairie dogs, Shortgrass Steppe																
9–Comanche-Cimmaron, CO/KS	BOGR, BUDA, ARsp	SPCO, MAPI, EUsp	ARFI	40.0	−2 to 2	13	51	44	0.2	0.3	1	0.3	30	34	2.2	1.3
Gunnison's prairie dogs, Colorado Plateau Grassland																
10–Aubrey Valley, AZ	BOGR, VUOC, zMUTO	SIAL, ERDI, PLPA	GUSA, ATCA	29.3	−2 to 2	15	14	13	19	17	0.4	0.4	61	53	1.1	0.4
White-tailed prairie dogs, Sagebrush Steppe																
11–Coyote Basin, UT	BRTE, PLJA, VUOC	SIAL, ALAL, PLPA	ARTR, GUSA	29.0	2 to 4	37	22	18	10	19	9	4	45	51	9.5	3.3
12–Moxa Arch, WY	ARsp, HOJU, POSE	LAOC, ARHO, PHHO	ARTR, ATGA	18.5	−2 to 2	10	10	5	6	4	13	16	66	77	2.7	1.5
13–Shirley Basin, WY	ELLA, PASM, POSE	PHHO, XYGL, ARHO	ARPE, ATGA, ARTR	25.3	−2 to 2	35	21	15	11	11	15	18	43	48	1.4	0.4

[a]Grasses: ARsp = Aristida spp.; BOCU = Bouteloua curtipendula; BOGR = Bouteloua gracilis; BRJA = Bromus japonicus; BRTE = Bromus tectorum; BUDA = Buchloe dactyloides; ELLA = Elymus lanceolatus; HECO = Hesperostipa comata; HOJU = Hordeum jubatum; PASM = Pascopyrum smithii; PLJA = Pleuraphis jamesii; PLMU = Pleuraphis mutica; POSE = Poa secunda; VUOC = Vulpia octoflora.

[b]Forbs: ALAL = Alyssum alyssoides; ARHO = Arenaria hookeri; COCA = Conyza canadensis; DEPI = Descurainia pinnata; DYPA = Dyssodia papposa; ERDI = Eriastrum diffusum; EUsp = Euphorbia spp.; HEHI = Hedeoma hispidum; LAOC = Lappula occidentalis; LOAR = Logfia arvensis; MAPI = Macharanthera pinnatifida; MEOF = Melilotus officinalis; PHHO = Phlox hoodii; PLPA = Plantago patagonica; SEDE = Selaginella densa; SIAL = Sisymbrium altissimum; SPCO = Sphaeralcea coccinea; VIAM = Vicia americana; XYGL = Xylorhiza glabriuscula.

[c]Shrubs: ARFI = Artemisia filifolia; ARFR = Artemisia frigida; ARCA = Artemisia cana; ARPE = Artemisia pedatifida; ARTR = Artemisia tridentata; ATCA = Atriplex canescens; ATGA = Atriplex gardneri; EPTR = Ephedra triurca; GUSA = Gutierrezia sarothrae; PRGL = Prosopis glandulosa.

[d]Mean annual precipitation.

[e]Palmer drought index for the month and year the site was sampled; >4 = extremely moist, 2 to 4 = moist, −2 to 2 = average, −3 to −4 = extreme drought.